



# Spatial patterns of nitrogen isotope ratios in forest soils are related to latitude and soil phosphorus concentration

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**Abstract** The aim of this study was to identify the parameters that affect the nitrogen (N) isotope ratio ( $\delta^{15}\text{N}$ ) in soils of temperate and boreal forests. We measured the  $\delta^{15}\text{N}$  in 30 soil profiles of temperate and boreal forests in Sweden and analyzed the relationships between  $\delta^{15}\text{N}$  in the soils and soil chemical properties as well as site characteristics. In addition, we conducted a meta-analysis of  $\delta^{15}\text{N}$  in the organic layer of European forests. We identified two types of  $\delta^{15}\text{N}$  patterns; in type D soils, the  $\delta^{15}\text{N}$  in the mineral soil decreases with depth, whereas in type C soil, the  $\delta^{15}\text{N}$  in the soil profile is almost constant. Type D soils had a significantly higher  $\delta^{15}\text{N}$  in the organic layer and upper mineral soil than type C soils, which is likely due to N isotope fractionation by ectomycorrhizal fungi in the topsoil. Type D soils were found in boreal forests, but not in temperate forests. They had a significantly lower atmospheric N deposition rate than type C soils, by a factor of 2.3, and a significantly higher phosphorus (P) concentration

of the organic layer than type C soils, by a factor of 1.5. We also found that the  $\delta^{15}\text{N}$  was negatively correlated with the N:P ratio of the organic layer ( $R^2=0.21$ ,  $p<0.001$ ). Across Europe, the  $\delta^{15}\text{N}$  of the organic layer was positively correlated with latitude ( $R^2=0.58$ ,  $p<0.001$ ), and negatively with mean annual temperature ( $R^2=0.52$ ,  $p<0.001$ ) and atmospheric N deposition ( $R^2=0.42$ ,  $p<0.001$ ). In conclusion, our results show that the  $\delta^{15}\text{N}$  of the organic layer and microbial N (re-)cycling in forest soils is positively related with latitude and the P concentration of the organic layer.

**Keywords** Nitrogen isotopes · Temperate forest · Boreal forest · Latitude · Phosphorus concentration · Atmospheric nitrogen deposition

## Introduction

The nitrogen (N) isotope ratio ( $^{15}\text{N}:^{14}\text{N}$ ) of soils reflects the accumulated effects of N cycling processes, and provides insights into long-term N dynamics in ecosystems at decadal timescales. Different processes of the N cycle affect the  $^{15}\text{N}:^{14}\text{N}$  ratio of soils (Nadelhoffer and Fry 1988; Högberg 1997; Baisden et al. 2002; Hobbie and Ouimette 2009). Plant biomass and plant litter are  $^{15}\text{N}$ -depleted compared to mineral soil (Högberg 1997; Michelsen et al. 1998; Hobbie and Colpaert 2003; Hobbie and Högberg 2012). Thus, soil horizons that receive high N inputs

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in the form of plant litter, such as the organic layer, are typically depleted in  $^{15}\text{N}$  relative to other parts of the soil (Högberg et al. 1996; Hobbie and Högberg 2012). Mycorrhizal fungi transfer  $^{15}\text{N}$ -depleted N to plants and concentrate  $^{15}\text{N}$  in their biomass, which is thus typically enriched in  $^{15}\text{N}$  compared to plant biomass and soil (Högberg 1997; Michelsen et al. 1998; Hobbie and Colpaert 2003). Furthermore, many other biotic N transformation processes discriminate against the heavier  $^{15}\text{N}$ , leading to  $^{15}\text{N}$  depletion of the product. For instance, nitrification and denitrification (Högberg 1997) and mineralization of organic N (Silfer et al. 1992) lead to N isotope fractionation. Nitrification in particular causes an enrichment of  $^{15}\text{N}$  in soil, if the process is associated with a loss of the resulting  $^{15}\text{N}$ -depleted N species from soil (Yoshida 1988). In addition, biotic  $\text{N}_2$  fixation can decrease the soil N isotope ratio (Högberg 1997; Scheibe and Spohn 2022).

The organic layer of forest soils is typically  $^{15}\text{N}$ -depleted compared to the mineral topsoil (Högberg et al. 1996; Hobbie and Ouimette 2009) due to the high input of  $^{15}\text{N}$ -depleted plant litter. The  $\delta^{15}\text{N}$  (that quantifies the  $^{15}\text{N}:^{14}\text{N}$  ratio) of the organic layer can be very low, and  $\delta^{15}\text{N}$  values of down to  $-12\text{‰}$  have been reported for forests in Belgium (Vervaet et al. 2002). Yet, for other regions, higher  $\delta^{15}\text{N}$  values of the organic layer have been found, for instance, between  $-6.5$  and  $-5.5\text{‰}$  in the Netherlands (Koopmans et al. 1997),  $-5.2\text{‰}$  in Switzerland (Bundt et al. 2001), between  $-2.1$  and  $-1\text{‰}$  in Denmark (Callesen et al. 2013),  $-1.5$  to  $+1.5\text{‰}$  in coniferous forests in Sweden (Hobbie et al. 2019), and  $-0.5$  to  $+3\text{‰}$  in Finland (Sah et al. 2006). Together, these findings indicate that there might be a positive relationship between the  $\delta^{15}\text{N}$  values of the organic layer and latitude.

In the mineral soil, contrasting patterns of the  $^{15}\text{N}:^{14}\text{N}$  ratio have been described (Hobbie and Ouimette 2009). In many mineral soils, the  $^{15}\text{N}:^{14}\text{N}$  ratio increases with increasing soil depth (Nadelhoffer and Fry 1988). For instance, in temperate forests in Chile,  $\delta^{15}\text{N}$  increased with increasing soil depth from about  $-2.5\text{‰}$  at 1 cm to about  $5\text{‰}$  at 50 cm depth (Boeckx et al. 2005). Similarly, in grassland soils in California,  $\delta^{15}\text{N}$  increased with increasing soil depth from about  $0\text{‰}$  at 1 cm depth to about  $5\text{‰}$  at 50 cm depth (Baisden et al. 2002). However, in some soils the  $\delta^{15}\text{N}$  decreases with increasing depth (Hobbie and

Ouimette 2009). For example, in deciduous forests in Austria, the  $\delta^{15}\text{N}$  below a depth of 50 cm decreased relative to the upper soil depth increments (Pörtl et al. 2007). Similarly, below a depth of 30 cm, the  $\delta^{15}\text{N}$  decreased relative to the upper soil depth increments in coniferous and deciduous forests in northeast China (Cheng et al. 2010).

The reasons for the different depth-related and latitudinal patterns of the  $^{15}\text{N}:^{14}\text{N}$  ratio in soils are not well known. Hobbie and Ouimette (2009) described two types of vertical  $\delta^{15}\text{N}$  patterns in soils. They hypothesized that under N limitation,  $\delta^{15}\text{N}$  increases in the topsoil across a small depth section and then does not change further with increasing soil depth. In contrast, in ecosystems with less N limitation and more inorganic N cycling,  $\delta^{15}\text{N}$  increases in the topsoil across a small depth section, and then decreases in the mineral subsoil (Hobbie and Ouimette 2009). In the following, we will refer to these two types of  $\delta^{15}\text{N}$  patterns as type C, whereby C stands for the almost constant  $\delta^{15}\text{N}$  in the mineral soil, and type D, whereby D stands for the decrease in  $\delta^{15}\text{N}$  in the mineral soil.

N cycling and the pattern of  $\delta^{15}\text{N}$  in soil might be related to the cycling of other nutrients, such as phosphorus (P), particularly in the organic layer, where the carbon-to-phosphorus ratio is very high compared to the mineral soil (Spohn and Chodak 2015). It has been shown, for example, that P addition led to a decrease in extractable ammonium due to increased microbial N immobilization in a temperate forest in Maine, USA (Salvino et al. 2019). Furthermore, several recent studies on Swedish forest soils found relationships between fungal activity, decomposition, and the P concentration. For instance, Almeida et al. (2023) showed that ectomycorrhizal growth was positively related to addition of the P-containing mineral apatite in a spruce forest. Spohn and Berg (2023) reported that P was transported into decomposing pine needle litter during the first 1.5 years of decomposition in temperate and boreal forests, likely by fungi. Furthermore, a recent study found that the organic layer stock of Swedish forest soils was negatively correlated with the organic layer P concentration, which might suggest a relationship between P concentration and decomposition (Spohn and Stendahl 2022).

The aim of this study was to identify the parameters that affect the pattern of the  $^{15}\text{N}:^{14}\text{N}$  ratio in

soils of temperate and boreal forests in order to better understand N cycling in forest soils. Following Hobbie and Ouimette (2009), we hypothesized that type D soils occur in regions with comparatively high atmospheric N deposition rates, whereas type C soils emerge in regions with lower atmospheric N deposition rates. To test this hypothesis and to identify under which conditions the two types of isotope patterns emerge, we measured the  $^{15}\text{N}:^{14}\text{N}$  ratio in 30 soil profiles of temperate and boreal forests in Sweden, located between  $56.5^\circ$  and  $67.1^\circ\text{N}$  and analyzed the relationship between  $\delta^{15}\text{N}$  patterns in the soils and other soil and site properties. In addition, we conducted a meta-analysis of  $\delta^{15}\text{N}$  of the organic layer of European forest soils to identify the factors that control the  $\delta^{15}\text{N}$  of the organic layer on a continental scale.

## Material and methods

### Structure of the inventory, sampling, and sample preparation

Soil samples were collected for the Swedish Forest Soil Inventory (SFSI). The SFSI in its current form started in 1983 and monitors the state of the Swedish forests with respect to soil and vegetation. It covers all of Sweden except for arable land and urban areas, and is conducted in collaboration with the Swedish National Forest Inventory. The inventory visits about 20,000 permanent plots over a 10-year period, sampling every year about 2000 plots distributed all over Sweden. Circular plots with 10 m radius are located in quadratic clusters on a triangular grid (Ranneby et al. 1987), which is denser towards the south of the country to account for the greater fragmentation of the landscape and a more diverse geology in the south of Sweden. Each quadratic cluster encompasses eight circular plots (or four in the southwestern region). At each of these circular plots, the tree stem diameter at breast height is determined for all trees higher than 1.3 m, and based on this the basal area is calculated. From the change in diameter over 5 years, the current stem growth rate of the trees at plot level is calculated. In addition, the stand age is determined from the stand history assessed by the repetitive inventory together with wood coring performed in the 1980s. The dominant tree type is classified according to the

following classes based on basal area: deciduous, mixed (which are mainly mixed coniferous forests with more than 50% coniferous trees), pine (*Pinus sylvestris* + *Pinus contorta*), and spruce (*Picea abies*). The understory vegetation is classified according to the Swedish site classification scheme by Hägglund and Lundmark (1977).

Soil sampling is carried out on a subset of the circular plots, i.e., organic layer sampling on c. 10,000 plots and mineral soil sampling on c. 4500 plots. The organic layer is sampled volumetrically using a 10 cm diameter corer in a  $3.14\text{ m}^2$  subplot within each circular plot throughout the entire depth of the organic layer (up to 30 cm depth), excluding the litter layer. To gain a sample volume of about 1.5 L, 1–9 volumetric samples are combined. In addition, a small soil profile is prepared in the subplot and mineral soil is collected at fixed depth intervals: 0–10 cm, 10–20 cm, and 55–65 cm. The soil order is determined according to the World Reference Base for Soil Resources (WRB; IUSS Working Group WRB 2014). The parent material of soil formation is classified at a depth of 20 cm in the mineral soil according to the following classes: well-sorted sediment, poorly-sorted sediment, till, bedrock and peat. The texture of the mineral soil samples is determined in the field according to the following classes: clay, fine silt, coarse silt, fine sand, sand, and coarse sand as well as gravel. In the laboratory, all soil samples are dried to constant weight at  $35^\circ\text{C}$ . The samples are homogenized and sieved ( $<2\text{ mm}$ ), and living and dead roots  $>1\text{ mm}$  diameter are removed from the mineral soil samples. The samples are weighed and the stock of the organic layer is calculated based on the weight of the  $<2\text{ mm}$ -fraction of the organic layer. Chemical and isotope analyses are carried out on the fine soil fraction ( $<2\text{ mm}$ ).

### Selection and description of plots

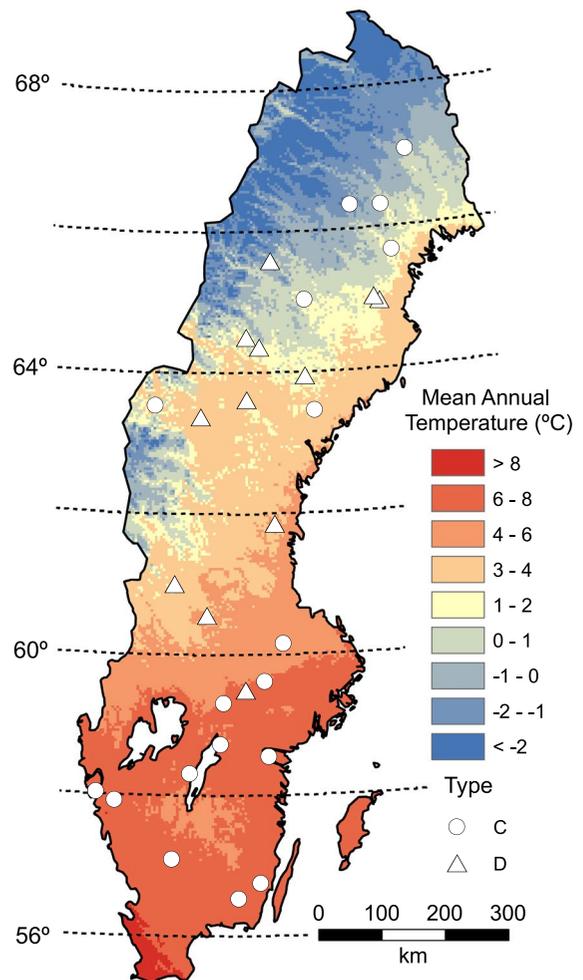
For the present study, we selected plots from the SFSI (1) that have been sampled between 2013 and 2018, (2) that were covered by forest with a long-term productivity  $>1\text{ m}^3\text{ year}^{-1}$  and a stand age  $\geq 60$  years, (3) that had the humus form mor or moder (which excludes peatlands and plots with humus form mull), and (4) for which data on the concentration of P in the parent material (at a depth of 50 cm) were available (Olsson et al. 1993). We excluded plots with a

stand age <60 years in order to exclude the effect of clear-cutting on soil properties in the dataset. We excluded plots with the humus form mull because at these plots, the mull humus is the A horizon and there is no organic layer according to the classification of the SFSI. Further, (5) we selected soils that have no eluvial horizon to minimize the effect of eluviation on the pattern of N isotopes in the soils of the dataset. This selection largely excludes Podzols, except for a few Podzols in the south of Sweden that have an accumulation horizon (which is why they classify as Podzols) but no eluvial horizon, likely due to past land use and soil disturbance.

The plot selection based on these criteria resulted in a total number of 30 plots. These 30 plots are a subset of the 309 plots described in Spohn and Stendahl (2022). The 30 plots are located between 56.5° and 67.1°N (Fig. 1; Supplementary Table S1). 16 plots are covered by spruce forest, 7 by pine forest, and another 7 by mixed pine-spruce forest (Supplementary Table S1). The mean stand age is 101 years, and the median age is 90 years. Concerning the organic layer form, 17 soils have the organic layer form mor with dominance of the F subhorizon (mor type 1), nine soils have the organic layer form mor with dominance of the H subhorizon (mor type 2), and three soils have the form moder. The mean depth of the organic layer is 10 cm and the median depth is 9 cm. Of the 30 soils, 18 soils are Regosols, five soils are Podzols, two soils are Gleysols, two Cambisols, two Arenosols, and one soil is an Umbrisol. In terms of parent material, eight soils are formed from well-sorted sediment, four from poorly-sorted sediment, and 18 from till. Concerning the texture, 12 soils are classified as fine sand, seven soils as coarse silt, five as sand, three as clay, two as fine silt, and one as coarse sand (Supplementary Table S1). The plots with ericoid understory vegetation [bilberry (*Vaccinium myrtillus*) and lingonberry (*Vaccinium vitis-idaea*)] tend to occur more frequently towards the North. Their mean latitude was 62.5°N, whereas the mean latitude of the sites with non-ericoid understory vegetation was 60.7°N.

#### Soil chemical and isotope analyses

The total C and N content were analyzed using an elemental analyzer (TruMac CN, LECO). The pH was determined in water (at a soil:water ratio of



**Fig. 1** Map depicting mean annual temperature (MAT), latitude, and the locations of the soils. The symbols (circle and triangle) indicate the  $^{15}\text{N}$  types C and D, respectively

1:2.5) using a Pt electrode (Aquatrode Plus Pt1000, Metrohm). Exchangeable cations (Ca, Mg, Na, K, and Mn) were extracted in 1 M ammonium acetate buffered at pH 7.00 and analyzed by inductively coupled plasma optical emission spectroscopy (ICP-OES; Avio 200, Perkin Elmer).

Total P in the parent material was determined on samples that were collected at the plots of the SFSI from the B/C and C horizon in the 1980s. The samples were ground, sieved (<2 mm), ignited and fused with lithium-metaborate, and subsequently, total P was determined by ICP (Olsson et al. 1993).

In addition to the variables determined for the SFSI, we measured total P in the organic layer,

total and organic P in the mineral soil at a depth of 0–10 cm as well as N and C isotopic ratios in all soil depth increments. Total P of the organic layer and the mineral soil at a depth of 0–10 cm was extracted in nitric acid and hydrogen peroxide (in a ratio of 1:3) in a microwave system (Ethos Easy, Milestone) according to the instructions of the manufacturer, and P was determined using ICP-OES (Avio 200, Perkin Elmer) after filtration of the extract. Organic P in the mineral soil at a depth of 0–10 cm was determined according to Saunders and Williams (1955) and Williams and Saunders (1956) as specified in Pansu and Gautheyrou (2007), using a continuous flow system (AA500, Seal). Total organic P was calculated as the difference in inorganic P between ignited and non-ignited samples.

The N and C isotopic ratios ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) were analyzed using continuous-flow isotope ratio mass Spectrometry on Flash EA 2000 via ConFlo IV open-split interface to a Delta V isotope ratio mass spectrometer (Thermo Fisher Scientific, Bremen, Germany) at the Stable Isotope Laboratory at SLU.

#### Climate data

Other data used in this study are mean annual temperature (MAT; from 2012), mean annual precipitation (MAP; from 2012) and total atmospheric N deposition (from 1998) retrieved from the Swedish Meteorological and Hydrological Institute. We assume that the atmospheric N deposition fluxes of the year 1998 are representative for historic atmospheric N deposition fluxes in Sweden during the last decades which were highest in the 1990s.

#### Data acquisition from published studies (meta-analysis)

In order to place our results about  $\delta^{15}\text{N}$  of the organic layer in Swedish forest soils in a larger geographical context, we analyzed published results about  $\delta^{15}\text{N}$  of the organic layer of European forest soils. For this purpose, we searched for peer-reviewed studies that report the  $\delta^{15}\text{N}$  of the organic layer of forest soils in Europe via Google Scholar, using the terms “ $\delta^{15}\text{N}$ ”, “forest soil”, “organic layer”, “forest floor”, “humus”, “natural abundance”, and “nitrogen isotopes”. Data about  $\delta^{15}\text{N}$  of the organic layer, latitude, MAT, MAP, and the atmospheric N deposition flux

where extracted from tables and figures of all studies that dealt with European forests. For the latter, the software DataThief was used. If the studies reported results about field experiments, only the control treatment was considered. We found twelve studies that reported the  $\delta^{15}\text{N}$  of the organic layer of forest soils located in Sweden, Finland, Denmark, Germany, the Netherlands, Belgian, Austria, Switzerland, and France (see Supplement B).

#### Data analysis

We classified the pattern of  $\delta^{15}\text{N}$  in the 30 Swedish forest soils as type C or type D. The letter D in type D stands for decrease and C in type C stands for constant. A soil was classified as type D if there was a steady decrease in  $\delta^{15}\text{N}$  in the mineral soil, i.e.,  $\delta^{15}\text{N}$  in 0–10 cm >  $\delta^{15}\text{N}$  in 10–20 cm and  $\delta^{15}\text{N}$  in 10–20 cm >  $\delta^{15}\text{N}$  in 55–65 cm. All other soils for which this was not true, were classified as type C.

In order to test whether type C and type D soils differ in soil chemical properties or site characteristics, we conducted Welch t-tests (with  $P=0.050$  considered as the threshold for significance) of the following soil chemical properties and site characteristics; Longitude, latitude, MAT, MAP, atmospheric N deposition, stand age, basal area, tree growth, dominant tree cover, soil texture, soil type, parent material, P concentration of the parent material, organic layer form, depth of the organic layer, organic layer stock as well as element concentrations and stocks (total C, N, P as well as exchangeable Ca, Mg, Na, K, and Mn) and pH of the organic layer and all three depths increments of the mineral soil and their C:N and C:P ratios. For the analysis of the categorical variables (dominant tree cover, organic layer form, soil texture, soil type, and parent material), different numbers were assigned to the different categories of each of these four variables.

In addition, we conducted ANOVA followed by Tukey’s test to examine if there are statistically significant differences in  $\delta^{15}\text{N}$  among the parent material classes, dominant tree cover classes, organic layer forms, and soil texture classes. We considered  $P=0.050$  as the threshold for significance. For the analysis of soil texture, the texture classes clay and fine silt were combined and the texture classes sand and coarse sand as well as gravel were also combined.

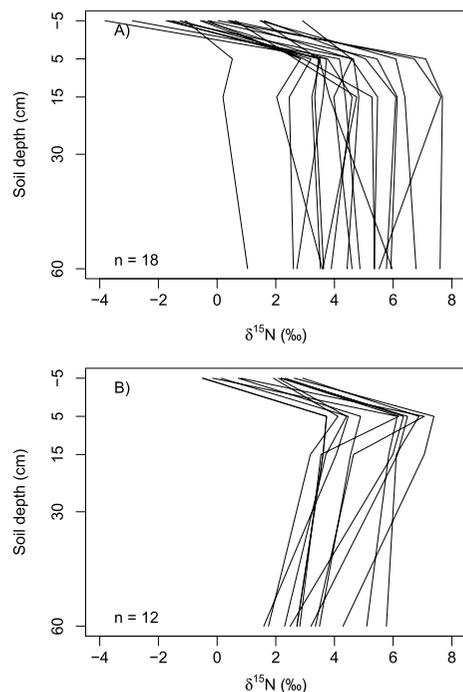
We performed discriminant analysis using the R package *mda* (<https://cran.r-project.org/web/packages/mda/index.html>), in which the assignment of the soils to type C and type D was predicted based on other variables in order to identify the most influential factors related with the formation of the two types. We included all variables in this analysis that differed significantly between type C and type D soils based on the Welch t-test (see above).

We conducted regression analyses to examine predictors of  $\delta^{15}\text{N}$  or the organic layer for the 30 Swedish forest soils and the soils of the meta-analysis. Furthermore, we conducted a multiple linear regression analysis with stepwise forward selection of predictor variables to predict the  $\delta^{15}\text{N}$  or the organic layer. In this analysis, the following variables of the 30 Swedish forest soils were included as potential predictors: longitude, latitude, MAT, MAP, atmospheric N deposition, stand age, basal area, tree growth, P concentration of the parent material, depth of the organic layer, organic layer stock as well as element concentrations (total C, N, P as well as exchangeable Ca, Mg, Na, K, and Mn), the C:N and C:P ratios, and the pH of the organic layer. All data analyses were conducted using R (version 4.1.1, R Core Team 2021).

## Results

Of the 30 soils, 12 soils were classified as type D, and the other 18 as type C (Fig. 2). The  $\delta^{15}\text{N}$  of the organic layer was significantly higher in type D than type C soils ( $P=0.002$ ), by  $1.7\text{‰}$  (Figs 2, 3a). In addition, the  $\delta^{15}\text{N}$  in 0–10 cm was significantly higher in type D than type C soils ( $P=0.007$ ), by  $1.5\text{‰}$  (Figs 2, 3b). In contrast, the  $\delta^{15}\text{N}$  in 55–65 cm was significantly lower in type D than type C soils ( $P=0.010$ ), by  $1.5\text{‰}$  (Figs 2, 3d). The N concentration did not differ significantly between the two types in any depth section (Supplementary Figure S1). The  $\delta^{13}\text{C}$  increased from  $-28.1\text{‰}$  in the organic layer to  $-26.6\text{‰}$  at a depth of 55–65 cm, irrespective of  $^{15}\text{N}$  type (C or D; Supplementary Figure S2).

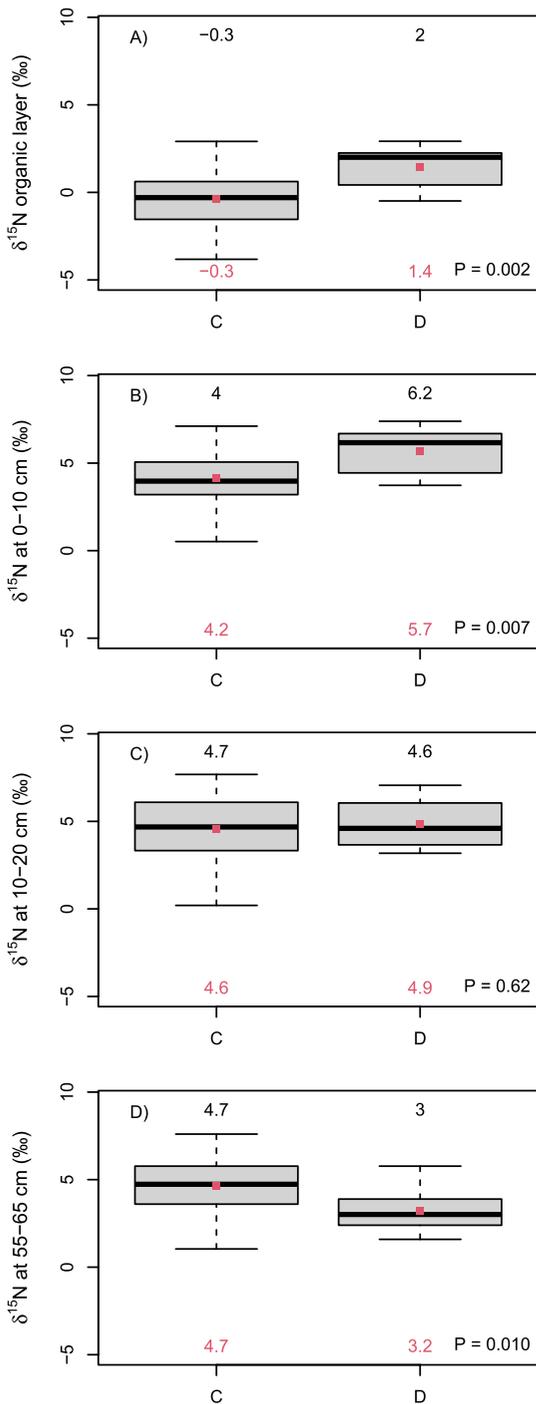
The mean atmospheric N deposition was significantly higher for type C than type D soils ( $P=0.002$ ), on average by a factor of 2.3 (Fig. 4a). The mean P concentration of the organic layer was significantly higher in type D than type C soils ( $P=0.020$ ), on average by a factor of 1.5 (Fig. 4b). The mean MAT



**Fig. 2**  $\delta^{15}\text{N}$  in type C (A) and type D (B) soils. The  $\delta^{15}\text{N}$  for the organic layer is indicated at  $-5$  cm,  $\delta^{15}\text{N}$  of the depth increment 0–10 cm is indicated at 5 cm,  $\delta^{15}\text{N}$  of the depth increment 10–20 cm is indicated at 15 cm, and  $\delta^{15}\text{N}$  of the depth increment 55–65 cm is indicated at 60 cm

was significantly higher for type C than type D soils ( $P=0.048$ ), on average by a factor of 1.9 (Fig. 4c). Furthermore, the mean latitude was higher for type D than for type C soils, but the difference between the two types was only marginally significant ( $P=0.050$ ; Fig. 4d). Type D soils were found in boreal forests between  $59.5$  and  $65.5^\circ\text{N}$ , at sites which mostly had a MAT between  $1$  and  $4^\circ\text{C}$ , but not in temperate forests. In contrast, type C soils were also found in temperate forest in the South of Sweden, and in the very North of Sweden above  $65.5^\circ\text{N}$  (Fig. 1).

Soils of both types (C and D) were found in all three forest types (spruce, pine, and mixed forest), and were found to have all three organic layer forms (Supplementary Table S1). The most dominant soil order in this dataset, Regosol, was found in type C and type D, while all (four) Podzols of the dataset classified as type C. Type C and D soils did not differ significantly ( $P>0.05$ ) in most analyzed variables, including longitude, MAP, texture class, stand age, basal area, tree growth, depth of the organic layer,



**Fig. 3**  $\delta^{15}\text{N}$  of the organic layer (a), the mineral soil at 0–10 cm depth (b), 10–20 cm depth (c), and 55–65 cm depth (d) depending on the  $^{15}\text{N}$  type ( $^{15}\text{N}$  type C:  $n=18$  and  $^{15}\text{N}$  type D:  $n=12$ ). Black numbers indicate the median, red dots and red numbers depict the arithmetic mean. The P value of the t-test comparing the two types is indicated at the right bottom of each panel

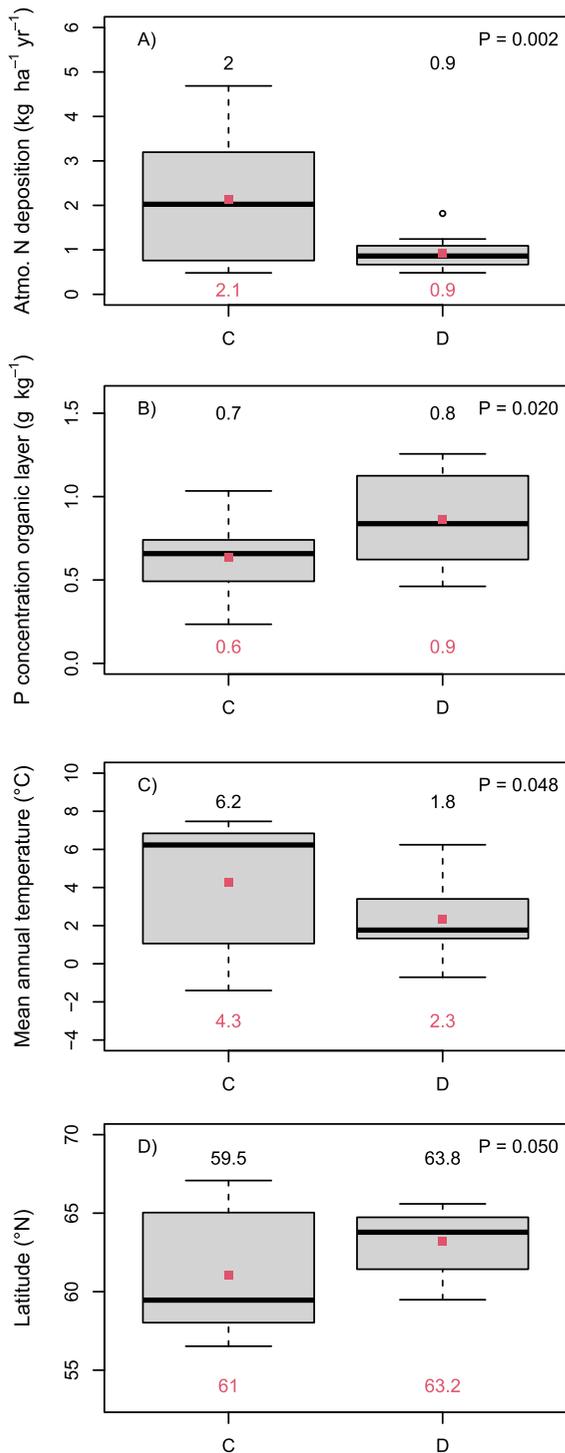
organic layer stock, P content of the parent material, organic and total P content at 0–10 cm depth as well as the N:P ratio of the organic layer and the stock of C, N and P in the organic layer. Further, soil pH, the organic C and total N concentration, the C:N ratio,  $\delta^{13}\text{C}$  as well as extractable Mn, K, Mg, and Ca did not differ significantly among type C and D in any of the four analyzed soil depth increments (organic layer and the three depth increments of the mineral soil).

The  $\delta^{15}\text{N}$  of the organic layer did not differ significantly ( $P > 0.05$ ) among the different parent materials, organic layer forms, different texture classes (see Supplementary Figure S3 for parent material). However, the  $\delta^{15}\text{N}$  of the organic layer was significantly higher ( $P < 0.05$ ) in soils with the parent material till than in soils with the parent material well-sorted sediment (Welch t-test). The  $\delta^{15}\text{N}$  of the organic layer did not differ significantly ( $P > 0.05$ ) among sites with and without ericoid understory vegetation.

The  $\delta^{15}\text{N}$  type was correctly predicted for 80% of the soils by discriminant analysis based on the atmospheric N deposition and latitude together (Table 1). Based on the atmospheric N deposition, latitude, the P concentration of the organic layer, and the parent material, the  $\delta^{15}\text{N}$  type was correctly predicted for 83% of the soils (Table 1). To correctly predict the  $^{15}\text{N}$  type for more than 83% of the soils, the  $\delta^{15}\text{N}$  of one depth increment needed to be included. Based on the atmospheric N deposition, latitude, the P concentration of the organic layer, MAT and the  $\delta^{15}\text{N}$  of the organic layer, the  $\delta^{15}\text{N}$  type was correctly predicted for 90% of the soils (Table 1).

We used a stepwise forward selection of predictor variables in a multiple regression model for predicting the  $\delta^{15}\text{N}$  of the organic layer (Table 2). The one-predictor model that produced the lowest Akaike information criterion (AIC) used the predictor N:P ratio of the organic layer. Adding further variables to the model reduced the AIC only to a very limited extent (Table 2).

The  $\delta^{15}\text{N}$  of the organic layer across all 30 soils was significantly positively correlated with latitude ( $R^2=0.12$ ,  $P=0.032$ ; Fig. 5a). Further, it was also positively correlated with the total P concentration of the organic layer ( $R^2=0.11$ ,  $P=0.041$ ; Fig. 5b) and negatively with the N:P ratio of the organic layer ( $R^2=0.21$ ,  $P < 0.001$ ; Fig. 5c). In contrast, the  $\delta^{15}\text{N}$  of the organic layer across all 30 soils was not significantly correlated ( $P > 0.05$ ) with the other soil



**Fig. 4** Atmospheric N deposition (a), P concentration of the organic layer (b), mean annual temperature (c), and latitude (d) depending on <sup>15</sup>N type (<sup>15</sup>N type C: n = 18 and <sup>15</sup>N type D: n = 12). Black numbers indicate the median, red dots and red numbers depict the arithmetic mean. The P-value of the t-test comparing the two types is indicated at the right side of each panel

chemical properties and site characteristics (including atmospheric N deposition, the depth of the organic layer, the organic layer stock, the C and K concentrations of the organic layer, the C:N ratio, and stand age).

We found that the N stock of the organic layer of the 30 soils was significantly negatively correlated with latitude ( $R^2=0.32$ ,  $P<0.001$ ; Fig. 6a) and positively with MAT ( $R^2=0.25$ ,  $P=0.003$ ; Fig. 6b). Furthermore the N:P ratio of the organic layer was negatively correlated with latitude ( $R^2=0.26$ ,  $P=0.002$ ; Fig. 6c).

We analyzed our data on  $\delta^{15}\text{N}$  of the organic layer in the 30 Swedish soils together with the data extracted from publications on  $\delta^{15}\text{N}$  of the organic layer of forest soils in other parts of Central and Northern Europe (Finland, Denmark, Germany, the Netherlands, Belgian, Austria, Switzerland, and France) with latitudes ranging from 68.2 to 47.3°N. We found a correlation between the  $\delta^{15}\text{N}$  of the organic layer and latitude ( $R^2=0.58$ ,  $P<0.001$ ,  $n=102$ ; Fig. 7a), the  $\delta^{15}\text{N}$  of the organic layer and mean annual temperature ( $R^2=0.52$ ,  $P<0.001$ ,  $n=111$ ; Fig. 7b) as well as between the  $\delta^{15}\text{N}$  of the organic layer and atmospheric N deposition ( $R^2=0.42$ ,  $P<0.001$ ,  $n=75$ ; Fig. 7c).

## Discussion

We observed and analyzed two types of  $\delta^{15}\text{N}$  patterns, which were previously described by Hobbie and Ouimette (2009), in temperate and boreal forest soils, and identified the conditions under which they form. We found that type D soils occur in boreal forests located between 59.5 and 65.5°N, but not in temperate forests. Type D soils had a significantly lower atmospheric N deposition rate and a significantly higher P concentration of the organic layer than type C soils. Furthermore, we found that the  $\delta^{15}\text{N}$  of the organic layer of forest soils is positively correlated with latitude in Sweden, and also across Central and Northern Europe.

### Type D soils: intensive microbial N transformation in the topsoil

The reason why type D soils had significantly higher  $\delta^{15}\text{N}$  values in the organic layer and the upper mineral soil (0–10 cm) than type C soils (Figs 2, 3) is likely

**Table 1** Results of the discriminant analysis based on the variables that differed significantly between the two  $^{15}\text{N}$  types (type C and type D)

Predictor(s)	Proportion of soils for which the $^{15}\text{N}$ type is correctly predicted (%)
Atmospheric N deposition	73
P concentration organic layer	70
Latitude	63
Mean annual temperature	60
Parent material	60
$\delta^{15}\text{N}$ organic layer	70
$\delta^{15}\text{N}$ in 0–10 cm	60
$\delta^{15}\text{N}$ in 10–20 cm	73
$\delta^{15}\text{N}$ in 55–65 cm	80
Atm. N deposition + latitude	80
Atm. N deposition + latitude + P concentration organic layer + parent material	83
Atm. N deposition + latitude + P concentration organic layer + mean annual temperature + $\delta^{15}\text{N}$ organic layer	90

Concerning the models with multiple predictors, the best model for each number of predictors is shown. The  $\delta^{15}\text{N}$  values were only included at the end of the analysis (when no increase in the prediction could be reached based on the first five predictors in the table). To correctly predict the  $^{15}\text{N}$  type for more than 83% of the soils, the  $\delta^{15}\text{N}$  of one depth increment needed to be included

**Table 2** Results of the stepwise multiple linear regression analysis with stepwise selection of predictor variables to predict  $\delta^{15}\text{N}$  of the organic layer. Each new predictor (+) is added to the previous ones (listed in the lines above)

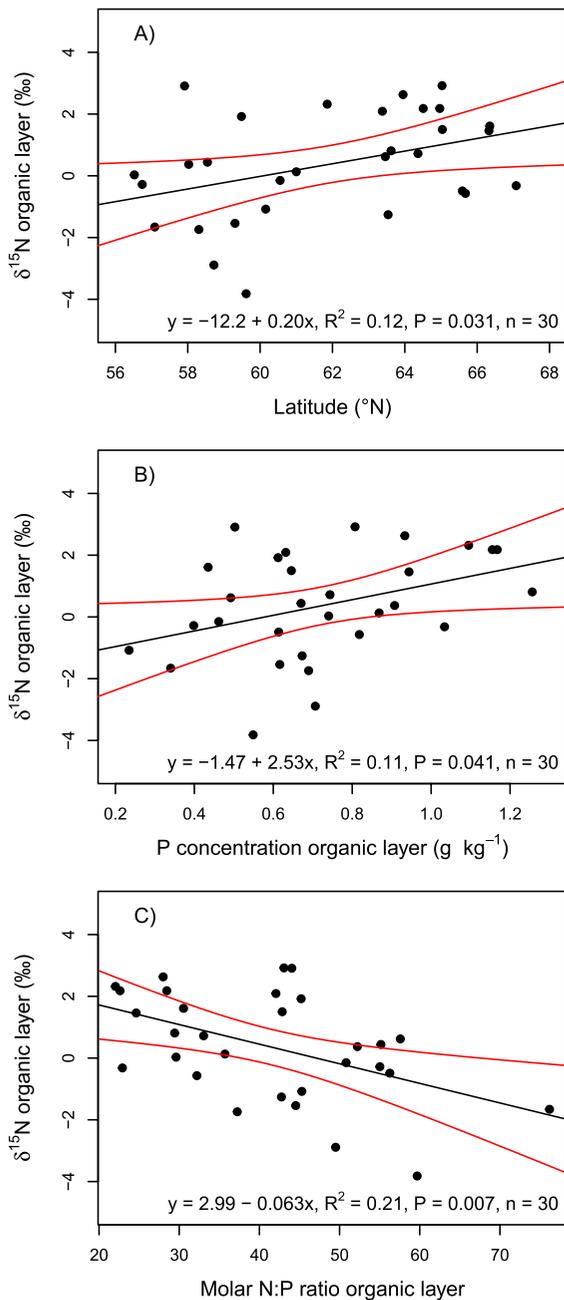
Predictors variables of $\delta^{15}\text{N}$ of the organic layer	Deviance residuals	AIC
N:P ratio organic layer	14.5	30.1
+ K concentration organic layer	7.1	29.0
+ Latitude	7.0	27.6
+ Basal area	7.0	25.8
+ Mean annual precipitation	9.4	21.6
+ P concentration organic layer	4.5	20.1
+ Organic layer stock	2.6	19.9

AIC Akaike information criterion

microbial processing of N that leads to enrichment of the heavier  $^{15}\text{N}$  isotope in the organic layer and mineral topsoil. Since ectomycorrhizal fungi contribute strongly to the soil microbial biomass and microbial activity in boreal forest soils (Högberg and Högberg 2002; Read et al. 2004), it seems likely that the  $^{15}\text{N}$  enrichment in the organic layer and mineral topsoil in type D soils compared to type C soils is mainly caused by ectomycorrhizal processing of N, i.e., delivery of  $^{15}\text{N}$ -depleted N to trees and accumulation of  $^{15}\text{N}$  in

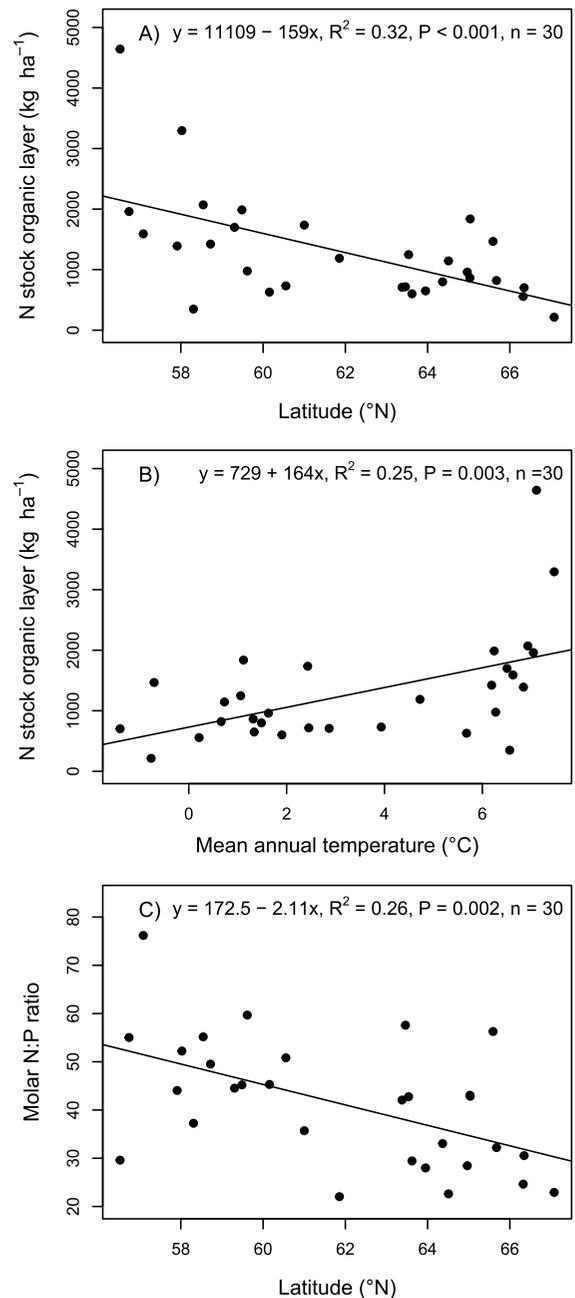
the fungal biomass (Hobbie and Colpaert 2003). Specifically, the higher  $\delta^{15}\text{N}$  of the organic layer in type D than in type C soils could be caused in the following ways; (1) larger rates of microbial N processing in type D than type C soils, potentially because a larger share of tree N uptake occurs through ectomycorrhizal fungi in these soils, (2) more frequently repeated (re-)cycling of N between the soil and the plants in type D than type C soils, and (3) stronger N isotopic fractionation by the species of ectomycorrhizal fungi present in type D soils compared to type C soils.

In type C soils, the  $\delta^{15}\text{N}$  at 55–65 cm depth was significantly higher than in type D soils (Fig. 3). This could be due to either substantial microbial N cycling in the subsoil of type C soils or, alternatively, transport of N with a relatively high  $^{15}\text{N}$  content from the topsoil to the subsoil, for instance through leaching. The latter seems particularly likely in the Podzols, which are all type C soils in our study, since Podzols form through leaching of organic material from the topsoil to the subsoil. It is noteworthy that we did not observe a strong, continuous increase in  $\delta^{15}\text{N}$  in the mineral soil in any of the studied profiles, in contrast to previous studies, for instance about forest soils in the temperate zone of Chile (Boeckx et al. 2005). This suggests that microbial N cycling in the northern



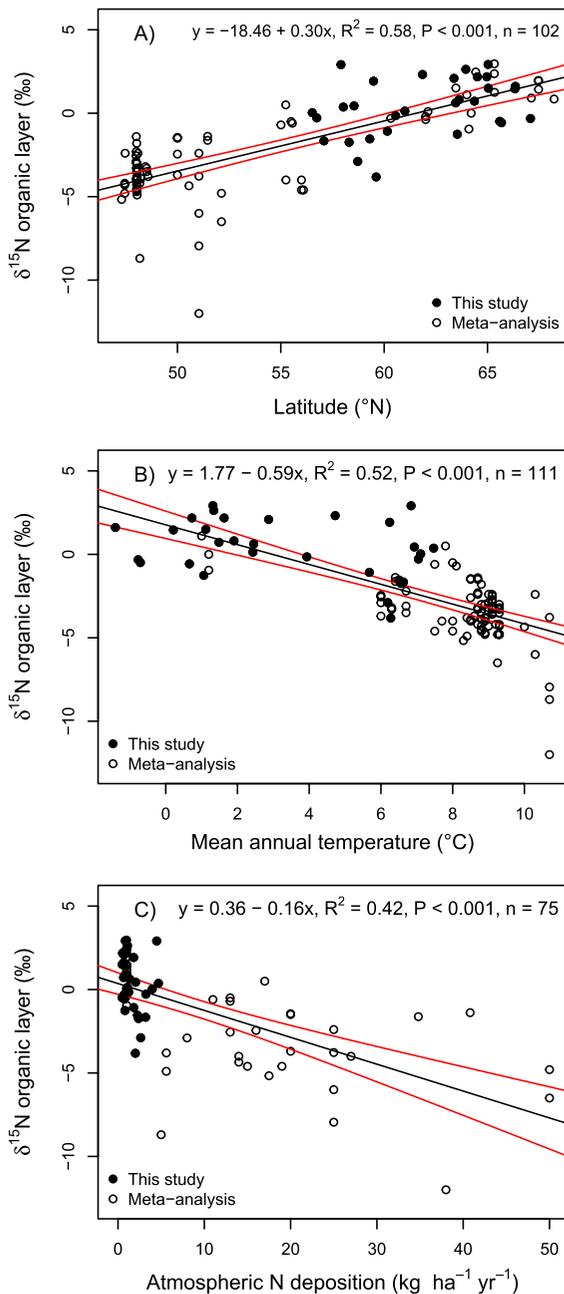
**Fig. 5**  $\delta^{15}\text{N}$  of the organic layer as a function of latitude (a), phosphorus (P) concentration of the organic layer (b), and the molar N:P ratio of the organic layer (c) across the 30 Swedish forest soils. The red lines indicate the upper and lower 95%-confidence interval

temperate and boreal zone is more strongly concentrated in the topsoil than in other forest soils. The fact that we found no substantial increase in the  $\delta^{15}\text{N}$  with



**Fig. 6** Nitrogen (N) stock of the organic layer as a function of latitude (a) and mean annual temperature (b) as well as the molar N:P ratio as a function of latitude (c) across the 30 Swedish forest soils

increasing soil depth also suggests that there was no major loss of microbially-transformed N from the subsoil since this would likely cause isotope



**Fig. 7**  $\delta^{15}\text{N}$  of the organic layer of the soils of the present study as well as of previous studies about forest soils in Central and Northern Europe as a function of latitude (a), mean annual temperature (b), and atmospheric nitrogen (N) deposition (c). The red lines indicate the upper and lower 95%-confidence interval

fractionation, and an increase in the abundance of the heavier  $^{15}\text{N}$  isotope in the subsoil.

### Type D soils have a high P concentration

Type D soils had a significantly higher P concentration in the organic layer than type C soils (Fig. 4b). In addition, the  $\delta^{15}\text{N}$  of the organic layer was significantly positively correlated with P concentration (Fig. 5b) and negatively with N:P ratio (Fig. 5c) of the organic layer across all 30 soil. This might indicate that P is beneficial for microbial N processing in these soils. The finding is supported by a study describing an increase in the growth rate of ectomycorrhizal fungi in response to P addition in a boreal spruce forest soil (Mayor et al. 2015). Our result that N cycling in forests soils depends on P availability is also corroborated by a study reporting that P addition led microbial N immobilization in a temperate forest in Maine, USA (Salvino et al. 2019). Further, our results are supported by a recent study showing that ectomycorrhizal growth was positively related with the presence of the P-bearing mineral apatite in a spruce forest in Sweden (Almeida et al. 2023).

### Type D soils have low atmospheric N deposition

Against the prediction by Hobbie and Ouimette (2009), the type D pattern was not associated with high N inputs but, on the contrary, with low atmospheric N deposition (on average  $0.9 \text{ kg ha}^{-1} \text{ year}^{-1}$ ; Fig. 4a). The reason for this could potentially be that atmospheric N deposition decreases the growth of ectomycorrhizal fungi (Bahr et al. 2013), and thus likely also ectomycorrhizal N cycling and fractionation of N isotopes. However, the threshold for negative effects of N inputs on conifer-associated ectomycorrhizal fungi is  $5\text{--}6 \text{ kg N ha}^{-1} \text{ year}^{-1}$  (Lilleskov et al. 2019), which is larger than the rates observed at the large majority of sites studied here. Hence, it seems likely that atmospheric N deposition has no (or only a minor) causal relationship with the  $\delta^{15}\text{N}$  patterns of the soils, and that the significant difference in the atmospheric N deposition rate between type C and type D soils emerges from the fact that type D soils occur at a certain latitudinal range (59.5 and  $65.5^\circ\text{N}$ , see Fig. 1), where atmospheric N deposition happens to be low.

$\delta^{15}\text{N}$  is positively correlated with latitude

The reason why type D soils occur at a specific latitudinal range might be that N is strongly recycled in forest ecosystems at this latitudinal range since the organic layer N stock at these sites is small (Fig. 6). Recycling of N is likely positively affected by the low N:P ratio at these sites (Figs 5c, 6c; see also Sect. “Type D soils have a high P concentration”). Furthermore, it might be that ectomycorrhizal fungi contribute more strongly to soil microbial N processing at these latitudes than in the temperate zone (Högberg and Högberg 2002; Read et al. 2004), which promotes N isotope fractionation (Högberg 1997; Michelsen et al. 1998; Hobbie and Colpaert 2003). Yet, beyond 65.5°N, we only found type C soils, but no type D soils. This might be due to a decrease in N cycling and abundance of ectomycorrhizal fungi at latitudes above 65.5°N, which could be caused by the very low temperatures at these latitudes (Figs 1, 6).

The  $\delta^{15}\text{N}$  of the organic layer across all 30 Swedish soils was significantly positively correlated with latitude (Fig. 5a), which is in accordance with a study showing that  $\delta^{15}\text{N}$  of the organic layer and tree foliage was positively correlated with latitude in forests in Finland (Sah et al. 2006). The reason for this relationship is likely twofold. First, the N stock of the organic layer (and probably of the entire ecosystem) decreases with increasing latitude (Fig. 6; see also Spohn and Stendahl (2022)), which very likely leads to enhanced recycling of N by biota in the high latitudinal ecosystems, and thus enrichment of the heavier  $^{15}\text{N}$  isotope. Second, in boreal forests, likely a larger proportion of N that trees take up passes first through ectomycorrhizal fungi than in temperate forests, leading to isotope fractionation. The finding that the  $\delta^{15}\text{N}$  of the organic layer in the 30 Swedish soils was not significantly correlated with atmospheric N deposition, suggests that the latitudinal differences in the  $\delta^{15}\text{N}$  of the organic layer are only weakly related to differences in atmospheric N deposition.

Across a larger dataset that comprises data from eight European countries, we found that  $\delta^{15}\text{N}$  of the organic layer was strongly and positively correlated with latitude and negatively with mean annual temperature (Fig. 7). The reason for this is likely that ecosystem N stocks and N inputs to the ecosystem are negatively correlated with latitude, leading to an increase in N recycling with increasing latitude. A

main reason why N stocks are negatively correlated with latitude seems to be that  $\text{N}_2$  fixation, which is the most important N input to the ecosystems, is positively related to temperature (Gundale et al. 2012; Rousk et al. 2013). However, the regulation of microbial  $\text{N}_2$  fixation in forest ecosystems is not yet well understood and requires further investigations.

## Conclusions

We analyzed two types of vertical  $\delta^{15}\text{N}$  patterns in temperate and boreal forest soils and identified the conditions under which they form. We found no support for the hypothesis that type D soils emerge in ecosystems with relatively high N supply, but instead, we observed that type D soils in Sweden only occur in boreal regions with very low atmospheric N deposition and a high P concentration of the organic layer. The formation of type D soils is likely caused by enhanced ectomycorrhizal N cycling and N isotope fractionation in the topsoil that leads to high  $\delta^{15}\text{N}$  values in the top of boreal forest soils. Our results show that N is more strongly transformed by microorganisms in boreal forests than in temperate forests, and that the intensive N transformation is related to a high P concentration of the organic layer. The positive correlation between  $\delta^{15}\text{N}$  of the organic layer and latitude across Central and Northern Europe indicates that the intensity with which N is microbially transformed in forest soils is positively correlated with latitude, likely due to a decline in the ecosystem N stock with increasing latitude.

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**Data availability** The data of the meta-analysis is displayed in Supplement B. All data will be made publically available once the manuscript is accepted for publication.

**Code availability** The R code will be made publically available once the manuscript is accepted for publication, and is available for editor and reviewers as an asset to this manuscript.

## Declarations

**Conflict of interest** The authors have no relevant financial or non-financial interests to disclose.

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## References

- Almeida JP, Menichetti L, Ekblad A, Rosenstock N, Wallander H (2023) Phosphorus regulates fungal biomass production in a Norway spruce forest. *Biogeosciences* 20(7):1443–1458
- Bahr A, Ellström M, Akselsson C, Ekblad A, Mikusinska A, Wallander H (2013) Growth of ectomycorrhizal fungal mycelium along a Norway spruce forest nitrogen deposition gradient and its effect on nitrogen leakage. *Soil Biol Biochem* 59:38–48
- Baisden WT, Amundson R, Brenner DL, Cook AC, Kendall C, Harden JW (2002) A multiisotope C and N modeling analysis of soil organic matter turnover and transport as a function of soil depth in a California annual grassland soil chronosequence. *Global Biogeochem Cycles* 16(4):82–91
- Boeckx P, Paulino L, Oyazún C, Cleemput OV, Godoy R (2005) Soil  $\delta^{15}\text{N}$  patterns in old-growth forests of southern Chile as integrator for N-cycling. *Isot Environ Health Stud* 41(3):249–259
- Bundt M, Jäggi M, Blaser P, Siegwolf R, Hagedorn F (2001) Carbon and nitrogen dynamics in preferential flow paths and matrix of a forest soil. *Soil Sci Soc Am J* 65(5):1529–1538
- Callesen I, Nilsson LO, Schmidt IK, Vesterdal L, Ambus P, Christiansen JR et al (2013) The natural abundance of  $^{15}\text{N}$  in litter and soil profiles under six temperate tree species: N cycling depends on tree species traits and site fertility. *Plant and Soil* 368(1): 375–392
- Cheng SL, Fang HJ, Yu GR, Zhu TH, Zheng JJ (2010) Foliar and soil  $^{15}\text{N}$  natural abundances provide field evidence on nitrogen dynamics in temperate and boreal forest ecosystems. *Plant Soil* 337(1):285–297
- Gundale MJ, Nilsson M, Bansal S, Jäderlund A (2012) The interactive effects of temperature and light on biological nitrogen fixation in boreal forests. *New Phytol* 194(2):453–463
- Hägglund B, Lundmark JE (1977) Site index estimation by means of site properties. *Studia forestalia Suecica* 138:1–38
- Hobbie EA, Colpaert JV (2003) Nitrogen availability and colonization by mycorrhizal fungi correlate with nitrogen isotope patterns in plants. *New Phytol* 157(1):115–126
- Hobbie EA, Ouimette AP (2009) Controls of nitrogen isotope patterns in soil profiles. *Biogeochemistry* 95(2):355–371
- Hobbie EA, Högborg P (2012) Nitrogen isotopes link mycorrhizal fungi and plants to nitrogen dynamics. *New Phytol* 196(2):367–382
- Hobbie EA, Chen J, Hasselquist NJ (2019) Fertilization alters nitrogen isotopes and concentrations in ectomycorrhizal fungi and soil in pine forests. *Fungal Ecol* 39:267–275
- Högborg P (1997) Tansley review no. 95  $^{15}\text{N}$  natural abundance in soil–plant systems. *New Phytol* 137(2): 179–203
- Högborg P, Högbom L, Schinkel H, Högborg M, Johannisson C, Wallmark H (1996)  $^{15}\text{N}$  abundance of surface soils, roots and mycorrhizas in profiles of European forest soils. *Oecologia* 108(2):207–214
- Högborg MN, Högborg P (2002) Extramatrical ectomycorrhizal mycelium contributes one-third of microbial biomass and produces, together with associated roots, half the dissolved organic carbon in a forest soil. *New Phytol* 154(3):791–795
- IUSS Working Group WRB (2014) World reference base for soil resources 2014, update 2015, International soil classification system for naming soils and creating legends for soil maps. World soil resources reports no. 106, FAO, Rome, 2015
- Koopmans CJ, Dam DV, Tietema A, Verstraten JM (1997) Natural  $^{15}\text{N}$  abundance in two nitrogen saturated forest ecosystems. *Oecologia* 111(4):470–480
- Lilleskov EA, Kuyper TW, Bidartondo MI, Hobbie EA (2019) Atmospheric nitrogen deposition impacts on the structure and function of forest mycorrhizal communities: a review. *Environ Pollut* 246:148–162
- Mayor JR, Mack MC, Schuur EA (2015) Decoupled stoichiometric, isotopic, and fungal responses of an ectomycorrhizal black spruce forest to nitrogen and phosphorus additions. *Soil Biol Biochem* 88:247–256
- Michelsen A, Quarmby C, Sleep D, Jonasson S (1998) Vascular plant  $^{15}\text{N}$  natural abundance in heath and forest tundra ecosystems is closely correlated with presence and type of mycorrhizal fungi in roots. *Oecologia* 115(3):406–418
- Nadelhoffer KJ, Fry B (1988) Controls on natural nitrogen-15 and carbon-13 abundances in forest soil organic matter. *Soil Sci Soc Am J* 52(6):1633–1640

- Olsson M, Rosén K, Melkerud PA (1993) Regional modeling of base cation losses from Swedish forest soils due to whole-tree harvesting. *Appl Geochem* 8:189–194
- Pansu M, Gautheyrou J (2007) Handbook of soil analysis: mineralogical, organic and inorganic methods. Springer Science & Business Media, Berlin
- Pörtl K, Zechmeister-Boltenstern S, Wanek W, Ambus P, Berger TW (2007) Natural  $^{15}\text{N}$  abundance of soil N pools and  $\text{N}_2\text{O}$  reflect the nitrogen dynamics of forest soils. *Plant Soil* 295(1):79–94
- Ranneby B, Cruse T, Häggglund B, Jonasson H, Swärd J (1987) Designing a new national forest survey for Sweden (no. 177)
- Read DJ, Leake JR, Perez-Moreno J (2004) Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. *Can J Bot* 82(8):1243–1263
- Rousk K, Jones DL, DeLuca TH (2013) Moss-cyanobacteria associations as biogenic sources of nitrogen in boreal forest ecosystems. *Front Microbiol* 4:150
- Sah SP, Rita H, Ilvesniemi H (2006)  $^{15}\text{N}$  natural abundance of foliage and soil across boreal forests of Finland. *Biogeochemistry* 80(3):277–288
- Salvino CJ, Patel KF, Fernandez IJ, Gruselle MC, Tatariw C, MacRae JD (2019) Phosphorus limits nitrogen dynamics in the O horizon of a forested watershed in Maine, USA. *Soil Sci Soc Am J* 83(4):1209–1218
- Saunders WMH, Williams EG (1955) Observations on the determination of total organic phosphorus in soils. *J Soil Sci* 6(2):254–267
- Scheibe A, Spohn M (2022)  $\text{N}_2$  fixation per unit microbial biomass increases with aridity. *Soil Biol Biochem* 172: 108733.
- Silfer JA, Engel MH, Macko SA (1992) Kinetic fractionation of stable carbon and nitrogen isotopes during peptide bond hydrolysis: experimental evidence and geochemical implications. *Chem Geol Isotope Geosci Sect* 101(3–4):211–221
- Spohn M, Berg B (2023) Import and release of nutrients during the first five years of plant litter decomposition. *Soil Biol Biochem* 176:108878
- Spohn M, Chodak M (2015) Microbial respiration per unit biomass increases with carbon-to-nutrient ratios in forest soils. *Soil Biol Biochem* 81:128–133
- Spohn M, Stendahl J (2022) Carbon, nitrogen, and phosphorus stoichiometry of organic matter in Swedish forest soils and its relationship with climate, tree species, and soil texture. *Biogeosciences* 19(8):2171–2186
- Vervaeet H, Boeckx P, Unamuno V, Van Cleemput O, Hofman G (2002) Can  $\delta^{15}\text{N}$  profiles in forest soils predict  $\text{NO}_3$  loss and net N mineralization rates? *Biol Fertil Soils* 36(2):143–150
- Williams EG, Saunders WMH (1956) Distribution of phosphorus in profiles and particle-size fractions of some Scottish soils. *J Soil Sci* 7(1):90–109
- Yoshida N (1988)  $^{15}\text{N}$ -depleted  $\text{N}_2\text{O}$  as a product of nitrification. *Nature* 335(6190):528–529

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